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SPORE CONDITIONS IN HYBRIDS AND THE MUTATION HYPOTHESIS OF DE VRIES[1]

EDWARD C. JEFFREY

(WITH PLATES XXII–XXV)

At the end of the sixteenth century CHARLES DE L'ECLUSE became professor of botany in the University of Leyden. He brought with him from Vienna to his new abode plants of the tulip, which had been introduced from Turkey into southeastern Europe. These formal plants he cultivated with great success in his own garden, and was fortunate in arousing a keen and even commercial interest among the phlegmatic Dutch; so much so that when the excitement was at its height, his garden was invaded and many of his choicest varieties stolen. Thus arose the famous "Tulipomania," which has been immortalized by DUMAS. Three hundred years later another Dutch botanist has become the author of another botanical sensation, which will doubtless also live in history. Professor DE VRIES has initiated the investigations on the genus *Oenothera* in connection with the hypothesis of mutation or saltatory origin of species. His discovery first that *Oenothera Lamarckiana* and subsequently that other species of the genus are capable of producing distinct so-called elementary species when cultivated on a large scale has very properly attracted a great deal of attention, particularly in the continent of North America, which prides itself, not altogether without reason, on its openness to new ideas. Thus it has come about that the genus *Oenothera*, and in particular *O. Lamarckiana*, has become the battleground of the mutation hypothesis on the botanical side. We have had during the past decade a veritable "Oenotheromania" comparable to the "Tulipomania" of three centuries ago.

There have been many objections raised to the mutation hypothesis of DE VRIES, particularly on the part of geneticists of

[1] Contributions from the Phanerogamic Laboratories of Harvard University, no. 70.

standing. The Englishman BATESON was apparently the first of these to record the opinion that *Oenothera Lamarckiana* was a hybrid, and he has been followed in this expression of opinion by many American scientific students of plant breeding. The greatest difficulties which have arisen in connection with *Oenothera Lamarckiana*, as studied by geneticists, have been in connection with its origin, and all herbaria, which could be supposed in any way to throw light on its original much discussed appearance, have been ransacked, without apparently a final or decisive result. The antecedents of this much disputed species, however, are now of less importance in view of the fact that other and possibly all species of *Oenothera* are likewise "mutating." The question of mutation, so far as it depends for its resolution on the study of *Oenothera*, has fortunately at the moment a much wider basis than the conditions found in any individual species of the genus, concerning the origin of which there may be serious doubt. As will be shown later in the present article, many of the species of *Oenothera*, if not all, are in the same peculiar and obviously extremely significant state as is *Oenothera Lamarckiana*. Attempts have been made to synthesize *O. Lamarckiana* from other American species, but this line of attack seems to lose some of its importance from the fact that almost any wild American *Oenothera* has apparently the same genetical peculiarities and the same power of "mutating" as has *Oenothera Lamarckiana* itself.

It has long been recognized on the part of scientific students of plant breeding that spore infertility is an important characteristic of hybrids. This view, originally expressed well on to a century ago, has lost none of its force in the intervening years. It is further recognized quite generally that relatively fixed hybrids may be produced. The opinion is at the present moment rapidly gaining ground, both on the zoological and on the botanical sides, that many of our wild species of plants and animals are in reality more or less fixed hybrids. In the case of plants we have peculiar advantages in connection with the recognition of this fact. We owe the most important results which have yet been produced on this continent, in this direction, to the studies of BRAINERD upon spontaneous hybrids of the violets and Rosaceae, for the most part

published in *Rhodora*. BRAINERD'S line of attack has been from the systematic, and, to a less extent, from the genetical side. It is the purpose of the present and succeeding articles to demonstrate evidence from the morphological side that hybridism is extremely widespread in nature, among the higher or angiospermous plants in particular, and that there is every reason to suppose that it has been an agency of great importance in *multiplying* species, although it is logically inconceivable in the present state of our biological knowledge that it could have presided at their *origin*.

In the following paragraphs the general conditions of sporogeny, so far as they are related to the matters under consideration, will be discussed and compared in the main groups of the embryophytes.

Beginning with the liverworts, the writer has examined a number of examples from the Marchantiales, Anthocerotales, and Jungermanniales (both acrogynous and anacrogynous), with the result that in no case which has come under his observation are there present any abnormal products in connection with spore-formation, unless the elaters can be considered abnormal structures in this respect. These elements, although undoubtedly derived from potential spore mother cells, are perfectly normal and have no significance in relation to a possible genetical impurity, any more than have the abortive spores and spore mothers found in the case of heterospory. In *Boschia*, as is shown in LEITGEB'S classic monograph, the elaters are represented by sterile cells without tracheary thickenings. In *Sphaerocarpus* the multinucleate condition of the elateriform cells clearly reveals their morphological derivation from spore mother cells. Fig. 1 illustrates the condition of the spores in *Marchantia polymorpha*, as an example of the liverworts. The elaters and spores are clearly seen, the former as spirally thickened bands, and the latter as dark or lighter spherical bodies. Where the spores are light in hue, the plane of section does not include the protoplasmic contents. Whether light or dark, the spores are of equal size and unshrunken.

An examination has been made of the sporogonia of a considerable number of the leafy mosses, with results, as far as they have gone, similar to those presented by the liverworts. The only genus examined which showed imperfect or abortive spores was

Sphagnum. As is well known, this genus is extremely variable, and the species are often difficult to distinguish. It appears accordingly not improbable that the abortion of spores sometimes found here may be correlated with hybridism in nature. Fig. 2 shows the homogeneous character of the spores in the common species *Polytrichum commune*. As is the case in the leafy mosses or Phyllobrya in general, there are no elaters present.

Numerous representatives of the Lycopodiales, heterosporous and homosporous, were examined and abortive spores were seen to be characteristically absent. Five species of *Lycopodium*, as well as *Phylloglossum*, *Psilotum*, *Tmesipteris*, *Selaginella*, *Isoetes*, *Lepidodendron*, *Spencerites*, etc., all yielded uniform results.

One species of *Equisetum* has long been recognized to be of hybrid origin, namely *E. littorale*, which from its anatomical and external features is a hybrid between *E. arvense* and *E. limosum*. It is one of the few conventionally recognized hybrid species, and is characterized by the large number of abortive spores which are found in its sporangia. Miss HOLDEN has recently published in *Science* an interesting account of abortive sporogeny, accompanied by blended anatomical features, in *Equisetum variegatum* var. *Jesupi*. It appears beyond question, from Miss HOLDEN'S work, that this variety is the result of a cross between *E. hiemale* and *E. variegatum*. It is further probable from her work that other recognized varieties of species of *Equisetum* are likewise hybrids in their origin. Fig. 3 represents a section through part of a sporangium in *E. hiemale*. Although all of the spores are not equally in the plane of section, it is clear that they are normal and unmingled with abortive individuals. In fig. 4 is shown a view of a section through a sporangium of *E. variegatum* var. *Jesupi*. Here there are practically no sound spores, unless one to the right of the figure can be considered sound. Even the spores of relatively large size and dark (protoplasmic) contents are abnormal. The smaller and abortive spores, which enormously predominate in the figure, have very scanty protoplasmic contents or none at all. Contrary to statements usually made in regard to abortive spores of *Equisetum*, the elaters are present, although not normally developed. They can be seen as circles bounding the spore proper

at an interval. They do not ordinarily separate into the usual bands, which is doubtless the reason their presence has not been heretofore recognized in the case of abortive *Equisetum* spores. Examination has been made of a number of sporangia of *Calamites*, and here, as in the living *Equisetum*, when uncontaminated by species crossing, the spores are perfect, although without the elaters, which appear likewise to have been absent in the mesozoic *Neocalamites*.

The ferns may next be considered, and for the purpose of the present investigation they may be divided into the Polypodiaceae and the remaining ferns. Taking the latter first, no evidence of hybridization in the recognized older groups of ferns has been found in this connection. Fig. 5 illustrates in section a sporangium of *Angiopteris evecta*. The spores are obviously all perfect. Examination of the genus *Marattia* has led to similar results. Other representatives of the Marattiaceae were not available. The Ophioglossaceae, as represented by the three genera *Ophioglossum*, *Botrychium*, and *Helminthostachys*, were studied and no evidence of abortive spores found in the sporangia. Representatives of the Gleicheniaceae and Schizaeaceae yielded similar results. *Osmunda regalis*, *O. cinnamomea*, and *O. Claytoniana* have strikingly perfect spores. *Todea barbara* showed similar conditions. Hymenophyllaceae, as represented by *Hymenophyllum* and *Trichomanes*, and the Cyathaceae by *Alsophila* and *Dicksonia*, yielded the same results. Of the heterosporous ferns, *Marsilia* and *Pilularia* were available, and these showed uniform spores. *Azolla* of the Salviniaceae has uniform spores.

Numerous cases of hybridism among the Polypodiaceae, accompanied by greater or less spore abortion, are known. The writer has personally examined only one hybrid fern of this group, namely the so-called *Adiantum hybridum* of gardeners. The spores here are apparently completely abortive, at any rate in greenhouse specimens. It will be unnecessary to enlarge upon the hybridism of the Polypodiaceae further, because recently an admirable statement has been published by BENEDICT,[2] in which he discusses the subject fully. He reports 11 natural hybrids for the eastern

[2] BENEDICT, R. C., Bull. Torr. Bot. Club **36**: 1909.

states, representing three genera. The status of some of these hybrids is beyond question because the cross has been repeated experimentally. Spore sterility is a marked feature in such cases. A large number of examinations of normal species has been made in the Polypodiaceae in the present connection, and uniformity of spore-formation has been found in such cases.

The Cycadales are of considerable interest from the evolutionary standpoint. The writer has been unable to find evidence of imperfection in the mature output of the sporangium. Two species of *Zamia*, as well as *Cycas revoluta*, *Stangeria paradoxa*, *Bowenia* sp., and *Microcycas*, were all examined with unvarying results. Fig. 6 shows part of a section through the microsporangium of *Zamia floridana*. The spores appear round where seen in face view, and somewhat crescentic when examined in profile. Both views may be seen in the illustration.

The monotypic *Ginkgo*, the sole survivor of a group once abundant in the Northern Hemisphere, has pollen which, in the large number of cases in which I have examined it, has proved to be singularly free from variation in size in the same sporangium. I have yet to see an imperfect microspore of *Ginkgo*. Fig. 7 shows the pollen as seen in a transverse section of the microsporangium. It will be noticed that the pollen grains present different appearances according to the plane of section and to the angle of incidence. The fact that the pollen in this interesting genus is winged as in *Pinus* can already be seen with the magnification employed in fig. 7. Fig. 8 presents a much more enlarged view, and the wings can be clearly discerned. It is curious that this striking feature of the pollen appears to have escaped notice. The wings bear the same relation to the cells of the microgametophyte within the pollen as they do in the Abietineae, and the number of prothallial cells in *Ginkgo* corresponds with that found in the Abietineae and not with the conditions found in the cycads, with which they are usually more nearly associated. A contribution from this laboratory dealing with the extremely striking features of resemblance between the Ginkgoales and the Abietineae will appear very shortly. The resemblance extends to nearly all the more important details of the reproductive and vegetative organs of the two groups.

The writer has had the opportunity of examining large quantities of coniferous material of all the subtribes, since his own studies have been particularly in this group. The Abietineae, Araucarineae, Podocarpineae, Taxineae, and Cupressineae in the broad sense, have all been studied in most of their genera, and in the case of the larger genera in a number of species. Perfection of pollen development was found to be characteristic of the microsporangia of this important group. The only case of pollen abortion which has come to light during the present investigation is that furnished by one species of *Abies*, to be described later. Fig. 9 illustrates the pollen conditions in *Araucaria Cooki*, cultivated in a greenhouse. It will be seen that the grains are all perfect, the difference of size being due to their greater or less inclusion in the plane of section. The greenhouse conditions have obviously not affected the morphological perfection of the pollen. Fig. 10 shows part of the same section under a higher degree of magnification. The numerous prothallial cells, which are a feature of the organization of the gametophyte produced in the pollen grains of the Araucarineae, can be seen.

The Gnetales have been studied in all their three surviving genera. *Welwitschia* has entirely perfect grains. The same statement holds for the three or four species of *Gnetum* which I have examined in this connection. Two species of *Ephedra* were examined, with the result that the pollen appeared to be without tendency to abortion. It is perhaps of interest to record, in this connection, that the pollen of *Ephedra* and *Welwitschia* are strikingly alike externally, both being characterized by spiral striation of the external coat of the oval grains. This feature was not found in the case of *Gnetum*. It has not been thought necessary to introduce an illustration of the microspores of the Gnetales, although several were prepared for this purpose.

The Monocotyledons may next be considered. Fig. 11 shows the pollen conditions in a wild species, *Iris versicolor*. The pollen is obviously perfect in development. Many hybrids of the various species of *Iris* are grown in gardens, in fact most of the more attractive cultivated irises are the result of hybridization. Fig. 12 illustrates the pollen conditions in a hybrid improvement

of *Iris germanica*. The species of *Iris* are usually quite free from any indication of hybrid contamination, with the possible exception of *Iris Hookeri*, which has not been fully studied. In fig. 12, the pollen is largely abortive and is reduced in amount, as is frequently the case in hybrids of all kinds.

Fig. 13 shows the pollen conditions in *Lilium canadense*. The grains are here quite perfect. Similar observations were made on *Lilium philadelphicum* and the common Easter lily. Fig. 14 illustrates the pollen abortion which is the usual condition in our cultivated *Narcissus*, nearly all of which are known to be of hybrid origin. The shriveled and abortive condition of a large number of the grains is quite evident. Fig. 15 pictures the condition of the pollen in *Lachenalia Nelsoni*, a plant very frequently grown in greenhouses in winter. This hybrid between two natural South African species of the genus was made by an English clergyman, in window culture, many years ago. Most of our garden tulips show their hybrid origin by large quantities of abortive pollen. A very large number of observations has been made upon monocotyledonous cultivated hybrids, with the unvarying result that hybridism was characteristically connected with a considerable amount of pollen degeneracy. On the other hand, monocotyledons grown in the greenhouse under obviously somewhat unnatural conditions, where of pure specific origin, showed, in all cases examined, good pollen. This was the case, for example, in species of *Gasteria*, *Agave*, etc.

We now advantageously turn our attention to the very large natural group of Dicotyledons. Here hybridization both natural and resulting from the intervention of man is extremely common. We may first consider with advantage the Rosaceae, in view of BRAINERD'S very interesting studies on this family. This investigator has shown that a great many natural hybrids of *Rosa* and *Rubus* occur in nature. The morphological observations made in this family entirely confirm BRAINERD'S results, and extend them in an apparently very interesting way, which will be summarized here, a fuller account being reserved for future publication. Not only are certain of the Rosaceae recognizable as hybrids, on account of their transitional external features of organization, Mendelian

phenomena, etc., but certain others, which have not revealed themselves as hybrids in these ways, are clearly such, as a result of the study of their spores. As an example let us take our mountain ashes (*Rosa* or *Rubus* furnish just as good illustrations, or in fact almost any of the larger genera of the Rosaceae in the Northern Hemisphere). In Europe and Asia it is generally recognized that the valid species of *Sorbus* have between them a number of natural hybrids. In the eastern and northern region of North America, we have two common species of mountain ash, *Sorbus americana* and *Sorbus sambucifolia*. These have been shown in connection with the present investigations to have pollen which is to a considerable degree abortive. The same observation has been made in regard to the European *Sorbus aucuparia*. In fact, the only species of *Sorbus* yet examined in this connection with perfect pollen is one growing in Japan. Or turning to another genus, *Prunus*, most of the species examined had imperfect pollen. Of the common species in New England investigated, the only one with perfect pollen was *Prunus serotina*, which flowers somewhat later than the others and is consequently phenologically isolated, just as is the case geographically with the Japanese *Sorbus* mentioned above. Illustrations of a similar nature could be given to an almost unlimited extent from studies on the Rosaceae, which are as yet far from complete. We have consequently to distinguish in the case of the Rosaceae, if the morphological features are taken into account as well as the data of systematic botany, three kinds of individuals, namely pure species, recognized species which from the condition of their pollen are in reality concealed hybrids or crypthybrids, and recognized hybrids. In some genera the multiplication of species through hybridization is very large; for example, over 4000 species of *Rubus* have been described in Europe, and in this country SARGENT and others have described a very large number of species of *Crataegus*.

Nearly all our common garden herbaceous dicotyledons, which from the nature of things are capable of hybridization, are hybridized. For example, we may take the carnations, the petunias, the phloxes, the chrysanthemums, the calceolarias, certain primroses, etc. Without concerning ourselves further with the dicotyledon-

ous cases of hybridization, we may now advantageously turn our attention to the consideration of the Onagraceae, the family which has supplied the famous case of *Oenothera Lamarckiana*. We may conveniently begin with our common garden fuchsias, which are known to be of hybrid derivation from *Fuchsia magellanica*, an inhabitant of southern South America. Fig. 19 shows the interesting pollen conditions found in certain cases in the cultivated *Fuchsia*. Many of the grains are shriveled and empty. In other instances still less pollen perfection was observed; in fact in some flowers there is practically no functional pollen and the anther sacs do not open, but dry up without dehiscence. In still other cases the pollen does not definitely shrivel up, but the grains are of very unequal size and contain a very scanty supply of protoplasm.

Let us now turn to the genus *Epilobium*. Our common fireweed, which inhabits somewhat generally the Northern Hemisphere, is illustrated in fig. 16. The figure includes all four anthers, which are laid open in the plane of section. It will be observed that the pollen in their cavities is perfect. The illustration is purposely made to show a large amount of pollen to demonstrate how normal the pollen development is in *Epilobium angustifolium*, the common willow herb, or fireweed. Fig. 17 shows a similar section of the flower of *Epilobium hirsutum*, the giant willow herb, which occurs near ballast heaps and is not uncommonly cultivated in New England. Even with the low magnification used, it becomes at once clear that the pollen development is abnormal, some of the grains being smaller and without protoplasmic contents. Fig. 18 shows a higher magnification of two of the anther cavities in this species, and on the left may be seen two sound grains and five abortive ones. On the right only abortive grains appear. The pollen in certain species of *Epilobium* occurs in tetrads, and in a smaller number of others it is quite separate at maturity. Those with the latter condition of the microspores are quite commonly put under the genus *Chamaenerion*. *Epilobium hirsutum* consequently shows evidence of hybridism in the presence of abortive spores in its anther cavities. For comparison with this type, the pollen development of the genus *Rhododendron* in the Ericaceae was examined. In a pure species, such as *Rhododendron catawbiense*,

all the grains are alike and all the tetrads are similar to one another. There are a number of hybrid derivatives of this species in cultivation. Two of these, named *R. Metternichi* and *R.* Mrs. H. W. Sargent, have been examined in this connection. The conditions found are exactly like those presented by *Epilobium* in the stricter sense. Some of the tetrads of pollen are entirely abortive, some only partially so, and in still others all the grains are perfectly developed. An extremely interesting fact in the present connection is the statement in standard European works on the genus *Epilobium* that its species all hybridize naturally with one another. In our specimen of *Epilobium hirsutum*, we obviously have to do with one of these hybrid conditions.

We are now, without further consideration of the Onagraceae, which would take us beyond the scope of the present article, in a position to consider advantageously the genus *Oenothera*. In fig. 20 is shown a portion of the anther contents of *Oenothera Lamarckiana*. Obviously the pollen is largely abortive. In fact, in his *Mutationstheorie*, DE VRIES does not conceal the fact that about one-third of the pollen of this species is shriveled and non-functional. Not only is this true of the species, but it is likewise true of its so-called mutants, some of the weaker of these, such as *O. nanella* and *O. lata*, having almost no good pollen. But it is not in *O. Lamarckiana* alone that one finds imperfect pollen. All of the numerous species of the genus which I have examined in this connection show more or less the same state of affairs. Fig. 21 illustrates the conditions in one of our commonest oenotheras, namely *O. biennis*. Even with the low magnification used, it is easy to see that the contents of the eight anthers shown photographically are far from normal. Fig. 22 shows the conditions as they appear under a higher magnification. Obviously here, as in *O. Lamarckiana*, a large amount of the pollen is sterile. All that can be said is that the genus *Oenothera* is in general, judging from its morphological condition, in a state of high genetical impurity. Fig. 23 shows a rather low magnification of several of the anthers of *O. Lamarckiana*. *O. grandiflora* is illustrated under the same degree of magnification in fig. 24. In this species the number of abortive pollen grains present is very small, and it is

in fact the least characterized by shriveled microspores of any species which I have yet had the opportunity to examine. It would seem consequently that it has either largely recovered from the effects of previous hybridization or else that the hybridizing ancestors have been less incompatible than those of, for example, *O. biennis*.

It is obvious that in the Onagraceae we have a peculiar condition, which is likewise present in other families of the angiosperms. Taking the Rosaceae as an illustration, there are in the various genera of this family numerous forms which are generally recognized on external characters as hybrids. Some of these conditions have recently been described by BRAINERD. In addition to admitted hybrids in the Rosaceae, there are a number of forms which very generally are admitted as good species on account of their relative constancy and the absence of observed intergrading types. In many of these recognized species, however, the morphological conditions, found in connection with the formation of the reproductive elements, are clearly those of hybrids. In view of the common occurrence of admitted hybridism in the family, these may properly be regarded as concealed or crypthybrids. The value of internal structure in the case of hybrids, as a key to the conditions involved, has not been sufficiently regarded in the past. It is obviously of the greatest importance in the Rosaceae. A further group of forms is found in the Rosaceae, where the reproductive structures are those of normal species elsewhere. That is to say, the pollen, the more readily investigated of the reproductive elements, is quite sound. This condition, for example, is characteristic of monotypic genera or genera with few well marked species (for example, *Kerria*, *Rhodotypus*, *Cydonia*, etc.). In genera with numerous species, contamination is very likely to be present, except in cases where the species are very distinct, or are isolated phenologically or geographically. For example, *Rosa* or *Sorbus*, geographically isolated in a mountainous or insular habitat, is genetically pure; while *Rosa* or *Sorbus* of continental or lowland origin is very likely to be genetically impure.

The principles cited above in the case of the Rosaceae have an obvious bearing on the conditions found in the Onagraceae.

Here, as in the larger family Rosaceae, we have the occurrence of admitted hybrids in certain genera (*Epilobium* and *Fuchsia*), side by side with recognized species. In other cases the recognized species have for the most part the same pollen conditions as those characteristic of hybrids. This state of affairs is found to a very large and striking degree in the genus *Oenothera*. Since the species of *Oenothera* to a very considerable extent, particularly those which have been used in investigations of a mutational or genetical nature (*O. Lamarckiana*, *O. biennis*, etc.), are under the strongest possible suspicion of hybrid origin, it follows that any conclusions drawn from their genetical behavior, in connection with the vexed problem of the origin of species, must be subject to a large degree of reserve. So far as the conduct of *O. Lamarckiana* and other species of the genus throws any light at all upon the species problem, it is in connection with the *multiplication* of species by hybridization, a very different matter indeed from the actual *origin* of species.

The relation of hybridization to "mutation" has recently been strongly emphasized for animals by GEROULD.[3] The reader is referred to this highly interesting and important contribution on the zoological side, for an expression of views very similar to the conclusions reached in the present article in the case of plants. In plants we have the great advantage of being able to a very large extent to supplement genetical and taxonomic data by the examination of internal organization.

The writer[4] has previously made a general statement on the questions here involved. GATES[5] has recently published an article in which he attempts to show that mutation and hybridization are independent phenomena. His conclusions seem to be fatally invalidated by the fact that his experiments were carried on upon *Oenothera* species and "mutants." The situation is apparently the same as would present itself if a chemist worked with impure chemicals or a physicist with mixed radiations.

[3] Species-making by hybridization and mutation. Amer. Nat. **48**: no. 570.

[4] The mutation myth. Science N.S. **39**:488–491. 1914.

[5] Breeding experiments which show that hybridization and mutation are independent phenomena. Zeitschr. Induktive Abst. und Vererb. **2**: Heft 4.

Summary

1. Spontaneous hybridization is comparatively rare among lower plants, but very common in the angiosperms.

2. A long recognized criterion of hybridism is sterility, partial or complete, of the reproductive cells. In plants this is recognized with particular ease in the case of the pollen.

3. In forms which are ordinarily recognized taxonomically as species, pollen infertility frequently indicates past genetical contamination.

4. In families such as the Rosaceae and the Onagraceae, we find grading into each other recognized species and recognized hybrids, having in common the character of partial or complete reproductive sterility, most easily recognized in the organization of the pollen.

5. This situation points inevitably to the hybrid origin of these abnormal species.

6. Species of this type may conveniently be called crypthybrids.

7. The species of *Oenothera* and many of those of *Epilobium* and probably those of *Fuchsia* as well are crypthybrids.

8. This condition must be clearly recognized in connection with any investigation in regard to the origin of species based on material of this sort, that is, on crypthybrids such as *Oenothera Lamarckiana*, *O. biennis*, etc.

9. Although there appears to be good evidence that hybridism has been an important cause of the multiplication of species, there seems to be no logical support for the view that it has to do with their actual origin.

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EXPLANATION OF PLATES XXII–XXV

PLATE XXII

FIG. 1.—Spores and elaters of *Marchantia polymorpha;* ×250.

FIG. 2.—Spores of *Polytrichum commune;* ×250.

FIG. 3.—Spores of *Equisetum hiemale;* ×200.

FIG. 4.—Spores of *E. variegatum*, var. *Jesupi*, a hybrid; ×200.

FIG. 5.—Spores of *Angiopteris evecta;* ×200.

FIG. 6.—Pollen of *Zamia floridana;* ×250.

PLATE XXIII

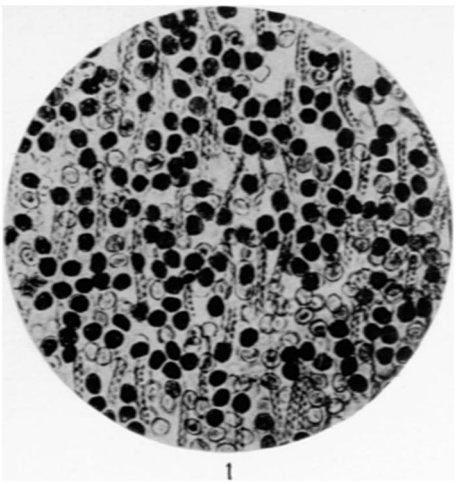
FIG. 7.—Pollen of *Ginkgo biloba;* ×250.
FIG. 8.—Pollen of the same; ×700.
FIG. 9.—Pollen of *Araucaria Cooki;* ×200.
FIG. 10.—Pollen of the same; ×400.
FIG. 11.—Pollen of *Iris versicolor;* ×150.
FIG. 12.—Pollen of *Iris germanica* hybrid; ×150.

PLATE XXIV

FIG. 13.—Pollen of *Lilium canadense;* ×125.
FIG. 14.—Pollen of *Narcissus* hybrid; ×250.
FIG. 15.—Pollen of *Lachenialia Nelsoni*, cultivated hybrid; ×250.
FIG. 16.—Central portion of flower of *Chamaenerion angustifolium;* ×25.
FIG. 17.—Part of flower of *Epilobium hirsutum;* ×25.
FIG. 18.—Anther of the same; ×125.

PLATE XXV

FIG. 19.—Part of anther of garden *Fuchsia* (hybrid of *F. magellanica*); ×200.
FIG. 20.—Part of anther of *Oenothera Lamarckiana;* ×200.
FIG. 21.—Flower of *O. biennis;* ×25.
FIG. 22.—Anther of *O. biennis;* ×200.
FIG. 23.—Anthers of *O. Lamarckiana;* ×50.
FIG. 24.—Anthers of *O. grandiflora;* ×50.



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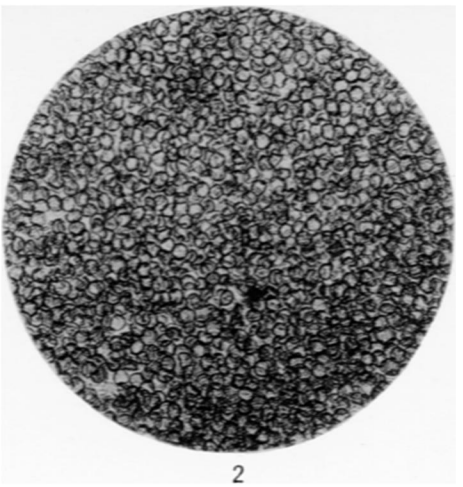

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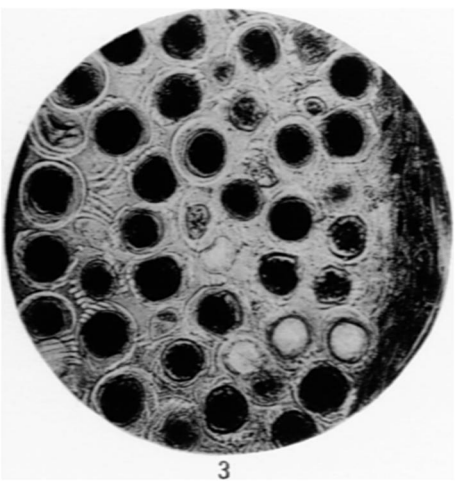

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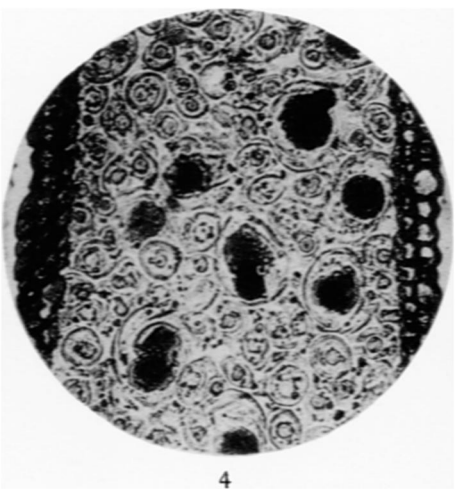

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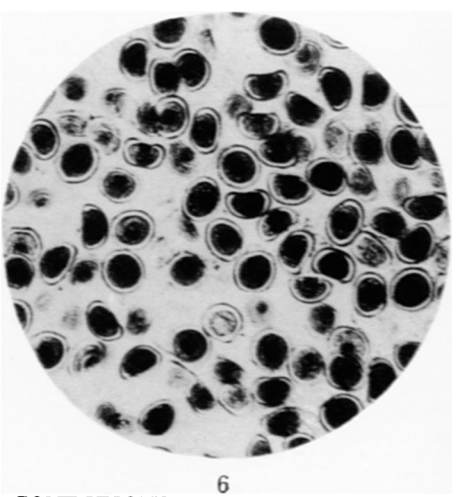

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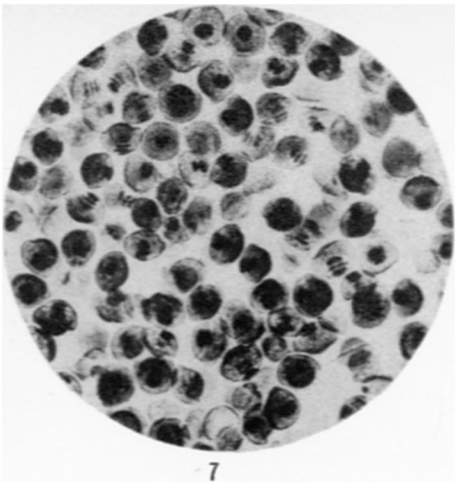
JEFFREY on SPORE CONDITIONS



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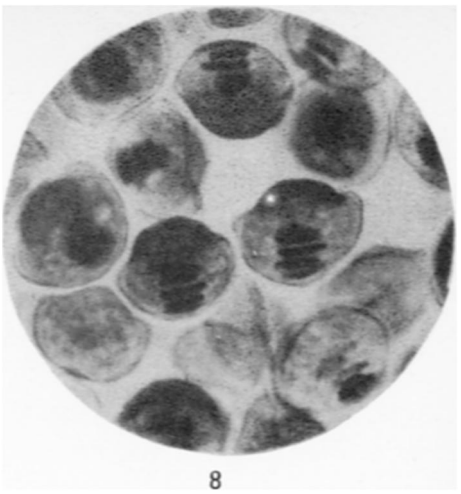

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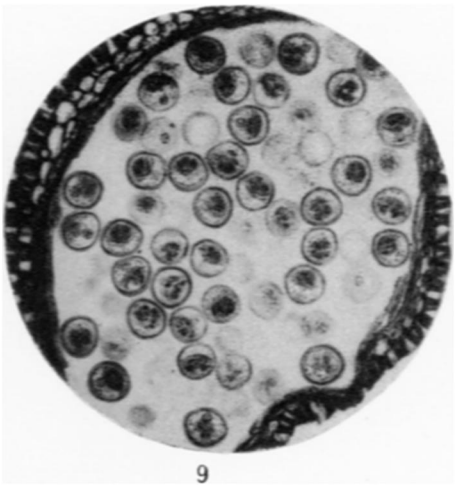

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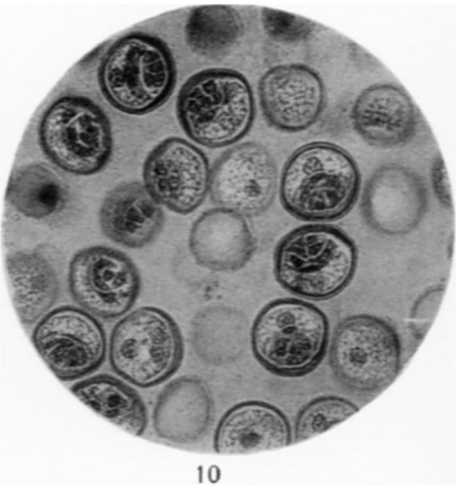

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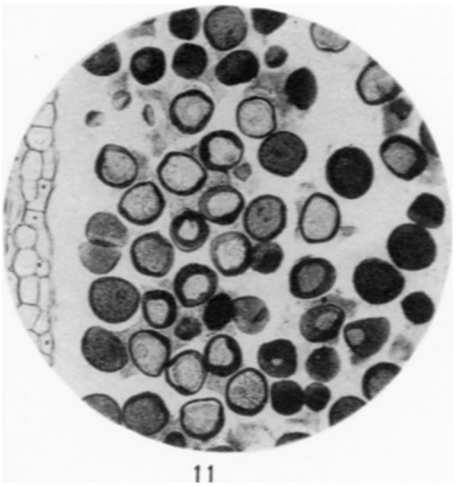

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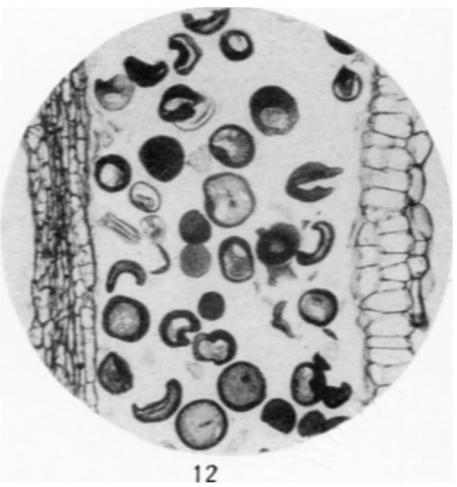

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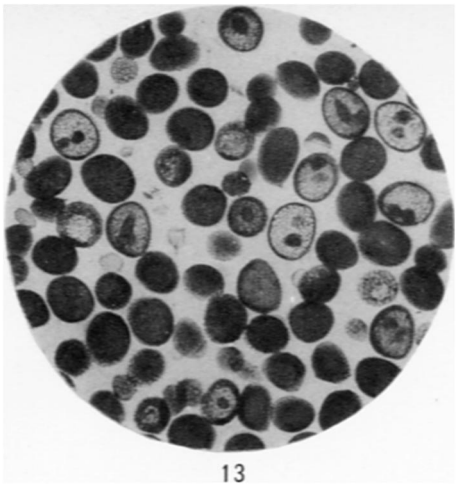
JEFFREY on SPORE CONDITIONS



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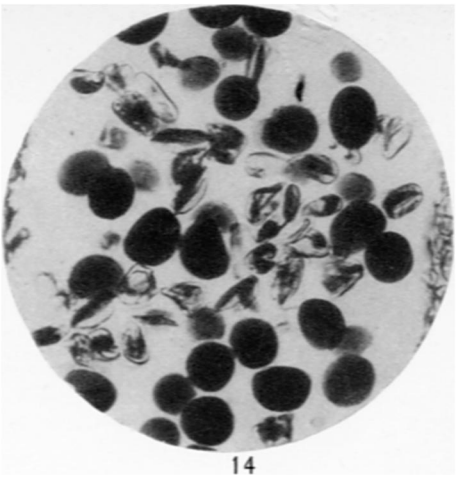

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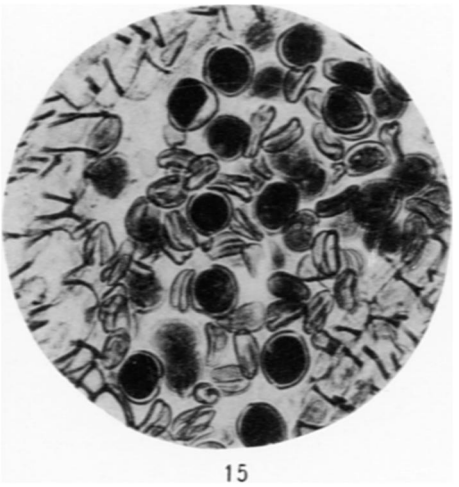

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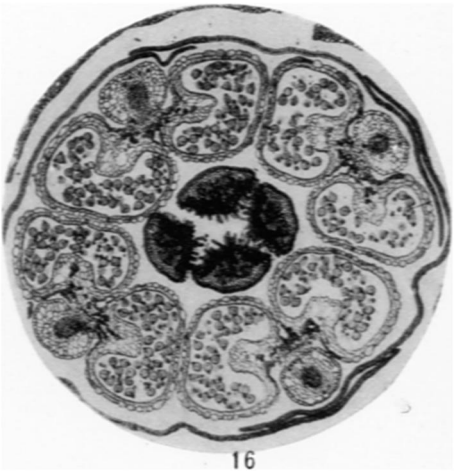

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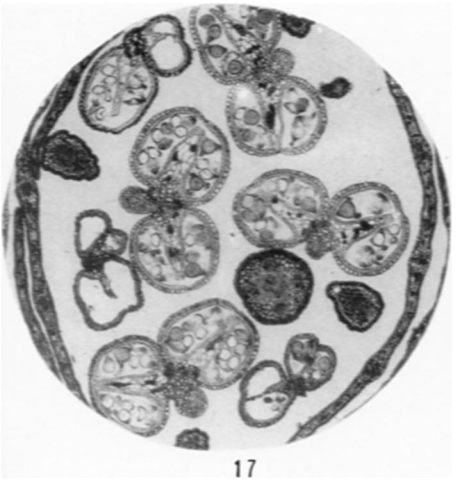

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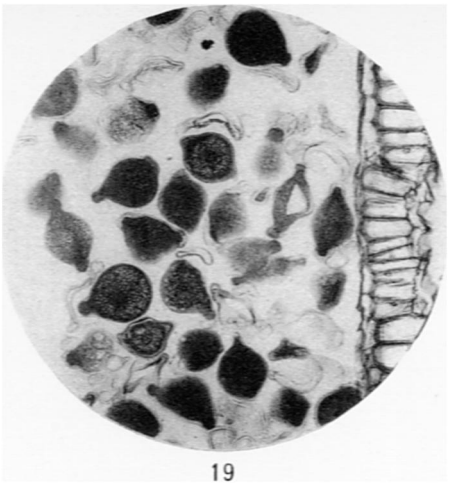
JEFFREY on SPORE CONDITIONS



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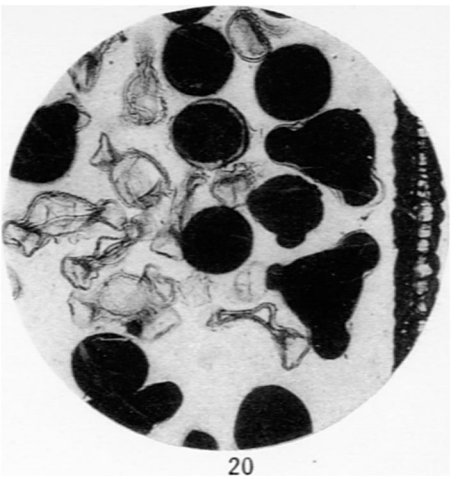

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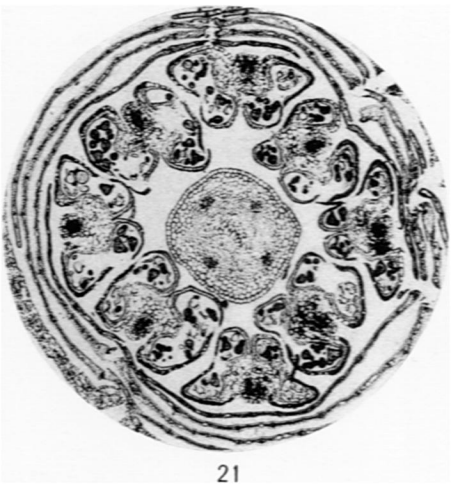

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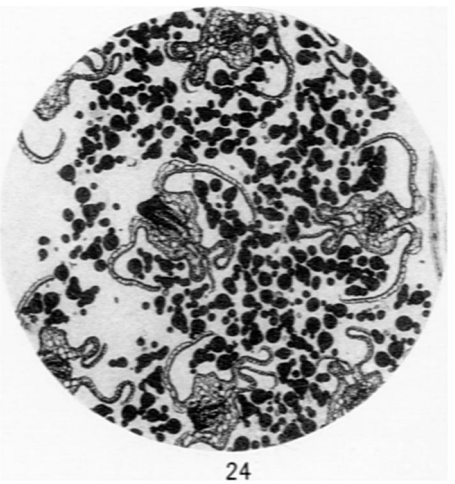

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JEFFREY on SPORE CONDITIONS